

BIOLOGY AND EVOLUTION OF THE NASAL REGION IN TREMATOPID AMPHIBIANS

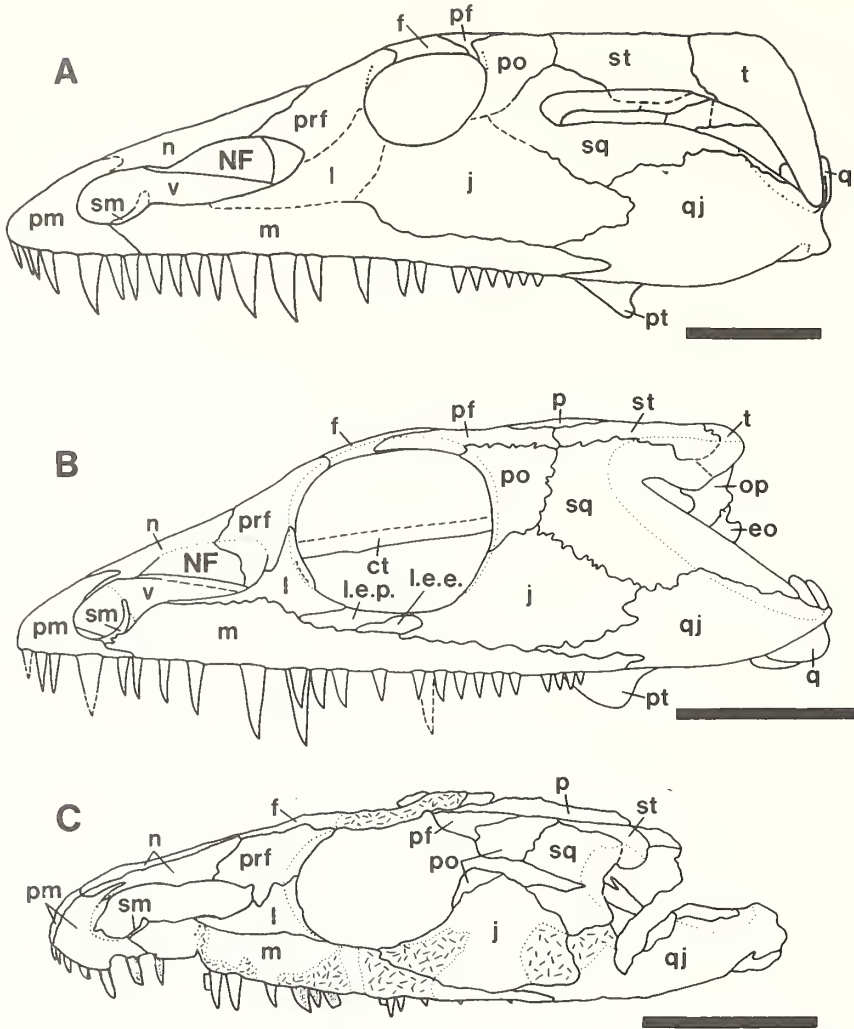
by DAVID W. DILKES

ABSTRACT. Postmetamorphic ontogeny of the nasal region in trematopid amphibians (Temnospondyli: Dissorophoidea) from the Lower Permian of Texas is characterized by the early appearance of a narial flange which is identical to that of an adult. Subsequent ontogenetic changes are the posterior expansion of the external naris, positive allometric growth of rostral length, and the development of caniniform teeth on the premaxillae and maxillae. It is hypothesized that the narial flange of dissorophoids, regardless of the details of its morphology, was an adaptation for terrestriality, and probably acted in a manner analogous to the primary concha of reptiles to enhance olfactory receptivity and improve the efficiency of moisture reclamation from exhaled air. Evolution of caniniform teeth in the Trematopidae apparently localized and increased cranial stresses in the rostrum during eating. Consequently, the plesiomorphic dissorophoid narial flange was modified in trematopids to fulfil an additional role of cranial reinforcement. Expansion of the external naris was a subsequent event, and probably a result, rather than a cause, of any alterations to cranial stresses. Existence of a salt gland in the expanded external naris is equivocal and not necessary for an interpretation of trematopids as terrestrial amphibians.

AMONG Palaeozoic tetrapods, the morphologically diverse temnospondylous amphibians of the clade Dissorophoidea are a favourite topic for palaeobiological discussion (e.g. Carroll 1964; DeMar 1968; Boy 1972; Bolt 1974a; Milner 1982; Bolt and Lombard 1985). Dissorophoids are limited traditionally only to taxa of the Carboniferous, Permian, and Early Triassic; Trueb and Cloutier (1991) on cladistic analysis included a monophyletic Lissamphibia within the Dissorophoidea. Considerable ontogenetic data are known for these fossil amphibians (e.g. Romer 1939; Boy 1974; Bolt 1974b, 1977a, 1977b, 1979; Olson 1985; Dilkes 1991) and have provided insights into the biphasic life history of dissorophoids, and into the origin of the Lissamphibia.

Two families of dissorophoids, the Dissorophidae and Trematopidae, will be discussed in this paper with the emphasis placed upon trematopids. In a re-evaluation of the Trematopidae (Dilkes 1990), a new genus, *Phonerpeton*, was erected on the basis of specimens first described by Olson (1941) and other, undescribed, material collected since his publication. Three species of temnospondyls are assigned currently to the Trematopidae (Berman *et al.* 1987; Dilkes and Reisz 1987; Dilkes 1990): *Phonerpeton pricei*, *Acheloma cummingsi* (senior synonym of *Trematops* (Dilkes and Reisz 1987)), and *Anconastes vesperus* (Text-fig. 1). Until recently, all known specimens of trematopids were restricted to the Early Permian of Texas, Oklahoma, New Mexico, and Ohio. A report of a trematopid from the Upper Rotliegendes of Germany (Martens 1990) was the first definitive occurrence outside North America. The Trematopidae is a monophyletic taxon diagnosed by the presence of caniniform teeth on the premaxilla and maxilla, an elongated external naris with a medially placed narial flange that contacts the antorbital bar, a median vomerine septum, an inflected medial rim of the adductor fossa, and by the absence of dermal sculpturing along the dorsal border of the otic notch (Dilkes 1990).

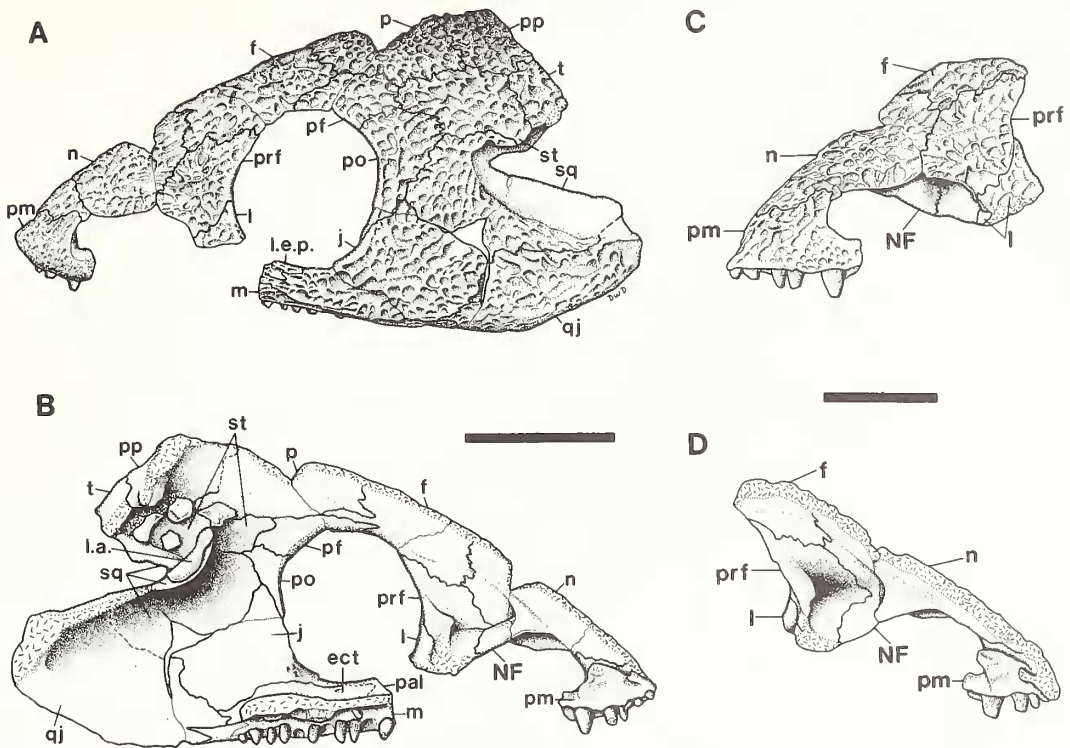
One of the most intriguing features of trematopids is the presence of an elongated external naris that superficially resembles a key-hole (Text-fig. 1). First recognized by Williston (1909), this character has been cited often as the defining feature of the family (Olson 1941; Vaughn 1969; Olson 1970; Eaton 1973). An elongated external naris has, however, evolved independently in the dissorophoid genera *Ecolsonia cutlerensis* (Berman *et al.* 1985) and *Mordex calliprepes* (Milner



TEXT-FIG. 1. Current members of the Trematopidae. A, *Acheloma cumminsi* (redrawn from Dilkes and Reisz 1987). B, *Phonerpeton pricei* (redrawn from Dilkes 1990). C, *Anconastes vesperus* (redrawn from Berman *et al.* 1987). Scale bars: A, C = 30 mm; B = 20 mm.

1986). Associated with the elongated external naris of trematopids is a distinctive, laterally concave bone within the nasal chamber known as the narial flange (Text-figs 1–3). Its pronounced lateral curvature permits an extensive contact with the antorbital bar. Superficially, the narial flange appears to be a single lamina, but it is composed of three separate bones; anteriorly, the first is from the nasal, the second from the prefrontal, and the third (and smallest) from the lacrimal (Bolt 1974a; Dilkes 1990). Contact between successive bones that comprise the narial flange varies from a short overlapping suture to a butt-like suture.

Taxa of the Dissorophidae also have a narial flange that is made of contributions from the same three bones (Bolt 1974a, 1974c), but the resultant morphology is different. The exceptionally well-preserved material of *Doleserpeton*, which according to Bolt (1977a, 1979) is a probable junior synonym of *Tersomius*, from the early Permian fissure fills near Richard's Spur, Oklahoma,

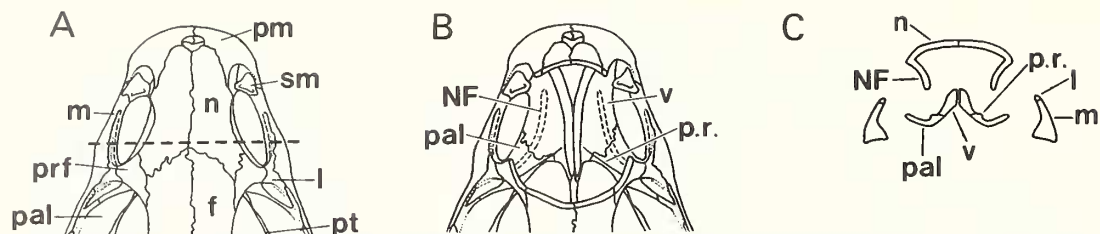


TEXT-FIG. 2. Partial left half of skull of small trematopid (cf. *Phonerpeton* sp.; MCZ 2475) lacking braincase and most of palate. A, exterior dorsolateral view. B, interior, ventromedial view. C, exterior of rostrum in anterolateral view. D, interior of rostrum in posteromedial view. Concave narial flange is visible in B, C and D. Scale bars: A-B = 20 mm, C-D = 10 mm.

provides the most information on the dissorophid narial flange. The contributions from the prefrontal and lacrimal are separate laminae that are similar in size and lie against one another to create a bilaminar structure which as a unit contacts the lamina of the nasal. The dissorophid narial flange lacks the pronounced lateral concavity of the trematopid flange. Details of the narial flanges of *Ecolsonia* and *Mordex* are unknown. Presence of a narial flange is restricted currently to trematopids and dissorophids (Bolt 1974a; Dilkes 1990).

To date, the only discussion of ontogeny for the Trematopidae was by Olson (1985) who compared a larval form with adult trematopids. He observed relative reductions in the sizes of the orbits and interpterygoid vacuities, and a posterior elongation of the jaw suspensorium. However, this larva is not a trematopid, though it can be identified confidently as a dissorophoid (Dilkes 1991). New ontogenetic data on the nasal region of trematopids was discovered during the course of the revision by Dilkes (1986) and its discussion herein is the first for the family.

The most recent proposal for the evolution of the trematopid nasal region was by Bolt (1974a) in which he hypothesized that the lateral expansion of a nasal salt gland led to the posterior elongation of the external naris as the region occupied formerly by bone became filled with glandular tissue. Bolt argued further that cranial stress patterns were modified in the rostrum by this narial elongation, and the narial flange of trematopids acquired its unique morphology to provide additional support for the rostrum. No further discussion on the evolution of the trematopid nasal region has followed, and Bolt's theory appears to have been generally accepted. However, no ontogenetic data were then available to him.



TEXT-FIG. 3. Rostrum of *Phonerpeton pricei*. A, dorsal view. B, rostrum with roof over nasal chamber removed to reveal dorsal surface of palate. Position of lower edge of the narial flange is shown by dashed lines. Note relative locations of the palatine ridge, narial flange and choana. C, schematic cross section through rostrum at level indicated by dashed line in A. Scale bar = 20 mm.

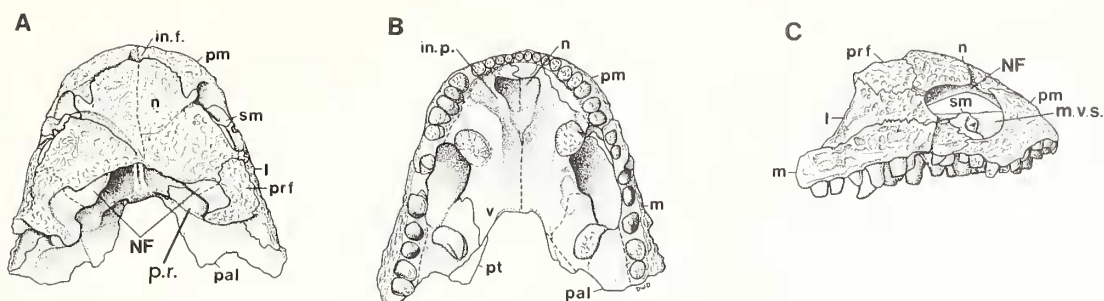
In this paper, the previously unpublished, new ontogenetic data from Dilkes (1986) are presented and an alternative evolutionary hypothesis, derived in part from Bolt (1974a, 1974c), is proposed for the trematopid narial flange and expanded external naris. In addition, a new physiological interpretation of the dissorophoid narial flange based upon analogous structures in extant ectotherms is presented.

MATERIAL

Discussion of the ontogenic growth of the trematopid skull is limited to the rostrum due to the nature of available specimens. All but one of the trematopids discussed in this paper are from the Lower Permian (Wichita Group) of north-central Texas. Terminology for their stratigraphical positions follows Hentz (1988) and Hentz and Brown (1987), and precise locality data are given in Dilkes (1990). MCZ (Museum of Comparative Zoology, Harvard University) 2531 was collected by Dr L. I. Price in 1937 from the Cowan Ranch locality in the Petrolia Formation (formerly Belle Plains Formation). Mr R. V. Witter collected MCZ 1417 and 1419 (holotype of *Phonerpeton pricei*) in 1936 and AMNH (American Museum of Natural History) 7150 in 1945 from the Archer City Bonebed in the Archer City Formation (formerly Putnam Formation). MCZ 2313 was collected by Dr A. S. Romer in 1952 from the Archer City Bonebed. The only specimen not from the Wichita Group is MCZ 2475 which was collected in the undivided Clear Fork Group (formerly Arroyo Formation) near West Coffee Creek, Baylor County, Texas.

Abbreviations used in the Text-figures

c.nas.pr.	cavum nasi proprium	l	lacrimal	pf	postfrontal
ch	choana	l.a.	lamina ascendens	pm	premaxilla
col	intercoronoid	l.e.e.	lateral exposure of ectopterygoid	po	postorbital
colI	precoronoid	l.e.p.	lateral exposure of palatine	prf	prefrontal
ct	cultriform process	l.div.	lateral diverticulum	pt	pterygoid
d	dentary	m	maxilla	q	quadrate
e.nar.	external naris	m.v.s.	median vomerine septum	qj	quadratojugal
e.nas.gl.	external nasal gland	mpal	maxillopalatine	s.n.	septum nasi
e.o.	eminentia olfactoria	n	nasal	sm	septomaxilla
ect	ectopterygoid	NF	narial flange	sp	splenic
eo	exoccipital	op	opisthotic	spp	postsplenic
f	frontal	org.J.	organ of Jacobson	sq	squamosal
i.gl.	intermaxillary gland	p	parietal	st	supratemporal
in.f.	internarial fenestra	p.c.	posterior concha	t	tabular
in.p.	internarial pit	p.r.	palatine ridge	v	vomer
j	jugal	pal	palatine		



TEXT-FIG. 4. Antorbital view of juvenile trematopid (MCZ 2531). A, dorsal view. B, ventral view. C, right lateral view. Narial flange of this juvenile is similar in size and shape to that of an adult as shown in Text-figure 2. Scale bar = 10 mm.

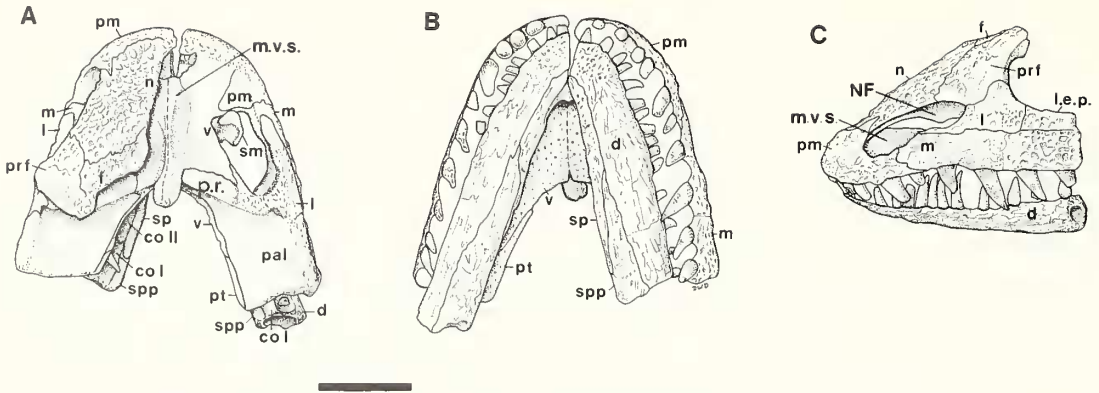
CRANIAL ONTOGENY OF THE TREMATOPIDAE

In his review of the Trematopidae, Olson (1941) assigned several skulls of small trematopids to two new species of *Acheloma*. The types of these species were assigned to *Phonerpeton pricei* by Dilkes (1990). Many of the skulls that were referred by Olson to his new species are incomplete and poorly preserved, but probably belong to *Phonerpeton*.

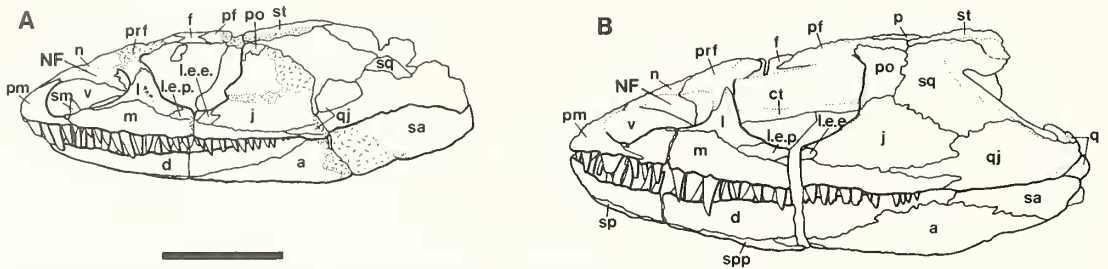
In addition to the referred skulls, several partial skulls of younger juveniles were collected, but not described by Olson (1941). A precise ontogenetic assessment of these skulls is difficult, but they can be interpreted as postmetamorphic by comparison with descriptions of juvenile dissorophoids (Milner 1982; Olson 1985; Dilkes 1991) judged to be larvae by the criteria of Boy (1974). The small trematopids discussed in this paper are much larger than the known larval dissorophoids, have more prominent dermal sculpturing, have palatal tusks on the vomer and palatine that are absent on larvae, and their cranial sutures are more tightly knit than in larvae. As these skulls are different sizes (and presumably different ontogenetic ages), it is possible to reconstruct a partial postmetamorphic growth series of trematopids. Unfortunately, these juvenile trematopid specimens are also fragmentary, and although found with adult skulls that can be identified as *Phonerpeton*, none of the diagnostic features of either *Phonerpeton* or *Acheloma* is preserved. Therefore, they will not be assigned to any particular genus. Nonetheless, the statements given below apply equally to both genera. Subadult and adult stages of *Phonerpeton pricei* will be used to complete the ontogenetic sequence because specimens are readily available.

The smallest available postmetamorphic specimens of trematopids (MCZ 2531) are two antorbital regions: one from an individual with an estimated midline skull length of 43 mm and the second with an estimated skull length of 53 mm. Most of the information given below is derived from the better preserved, larger specimen (Text-fig. 4). Both are gently convex anteriorly in dorsal view. An oval internarial fenestra is situated on the rostrum at the midline junction between the premaxillae and nasals. The internarial fenestra opens ventrally into a deep internarial pit that is formed by the dorsal deflection and separation of the vomers. A median vomerine septum separates the two nasal chambers, but does not contact the roof of the rostrum.

The narial flange of MCZ 2531 is a massive sheet of bone that projects deeply into the nasal chamber and contacts the antorbital bar just in front of the orbit. No sutures are visible on the narial flange; nonetheless, it is virtually identical to the concave flange of adult trematopids. The posterior expansion of the external naris of MCZ 2531 is only slightly greater than the size of the true narial opening and, therefore, does not meet the narial flange as it does in adult trematopids (Text-fig. 1A-B). The prefrontal is excluded from the external naris as an apparent consequence of



TEXT-FIG. 5. Antorbital region of juvenile trematopid MCZ 1417. A, dorsal view. B, ventral view. C, left lateral view. Scale bar = 10 mm.



TEXT-FIG. 6. *Phonerpeton pricei*. A, MCZ 1419. B, AMNH 7150. Both specimens are shown in left lateral view. Differentiation of caniniform teeth is apparent in AMNH 7150 relative to MCZ 1419. Scale bar = 20 mm.

the small narial expansion. The marginal teeth are large, but lack the caniniform specialization that is characteristic of adult trematopids.

A third antorbital region (MCZ 1417; Text-fig. 5) from a slightly larger individual (estimated midline skull length = 56 mm) has a more elongate and narrower antorbital region than that of MCZ 2531. The posterior division of the naris is larger and considerably closer to the contact of the narial flange and antorbital bar. Marginal teeth are differentiated to the state of canine peaks as defined by Chase (1963).

The holotypic skull of *Phonerpeton pricei* (MCZ 1419; Text-fig. 6A) with a skull length of 73 mm has a laterally constricted antorbital region with slight expansions on the premaxilla and maxilla for canine peaks. The posterior elongation of the naris is relatively greater than that of MCZ 1417 and reaches the narial flange. Development of caniniform teeth has not, however, proceeded beyond that of MCZ 1417 and it is herein considered to be a subadult.

AMNH 7150 (Text-fig. 6B; Dilkes 1990, fig. 3) is from an osteologically mature individual (skull length = 77 mm) as shown by the advanced ossification, rugosity of dermal sculpturing, and highly interdigitated cranial sutures. The shape of the antorbital region and the expansion of the external naris are similar to that of MCZ 1419. Caniniform teeth are fully differentiated.

These specimens enable us to recognize several stages in the postmetamorphic ontogenetic growth of the trematopid skull. One early stage is the formation of a narial flange which is identical in position and shape to that of an adult. In fact, a narial flange may appear as early as the larval stage. A specimen of a larval dissorophoid has the nasal portion of a narial flange clearly visible within its left elongated external naris (Dilkes 1991). It is conceivable that dissorophoids and trematopids

had similar premetamorphic growth patterns and the narial flange might have developed as early as the late larval stage in both families. As postmetamorphic growth in trematopids progressed, the external naris expanded posteriorly to contact the flange along the antorbital bar, and the antorbital region changed from a broadly rounded outline in dorsal view to one that is more elongate and narrower. Expansion of the external naris in adult specimens of trematopids does not occur posterior to the contact of the narial flange with the antorbital bar. Hence, it can be inferred that this contact between the narial flange and antorbital bar is the limit for the expansion of the external naris. Since the expansion of the external naris is observed to occur together with the elongation of the antorbital region, one may infer further that major allometric growth of the rostrum halts when this limit is reached. Additional isometric growth of the entire skull would probably occur after the major allometric changes were finished as suggested by a slightly larger skull (MCZ 2313, skull length = 88 mm) of *Phonerpeton* that has similar proportions to that of AMNH 7150. The final ontogenetic stage is the completion of premaxillary and maxillary caniniform teeth.

EVOLUTION OF THE TREMATOPID EXTERNAL NARIS

Previous research

The possible function of the elongate external naris of trematopids has been the subject of speculation by Williston (1909), Olson (1941), and most recently Bolt (1974a). Williston (1909) believed that the posterior division was an antorbital vacuity and the anterior division was the functional naris. His interpretation was based apparently upon a superficial resemblance between the posterior portion of the external naris and the characteristic antorbital fenestra of archosaurian reptiles. Olson (1941) also referred to the posterior portion as an antorbital vacuity, but rejected the notion of an unknown gland lodged within the vacuity. This statement was probably a reference to Broom (1913) who first suggested that the archosaurian antorbital vacuity housed a gland. Olson argued that the large medial chamber with the narial flange (his 'descending septum of the nasal') communicated only with the anterior division of the external naris whereas the posterior division opened only into the choana. The medial chamber was thought to contain a vomeronasal organ and, thus, was concerned only with olfaction. The posterior division acted as the functional narial opening. This interpretation is, however, refuted by the location of the septomaxilla which is found primitively in tetrapods along the posterior margin of the external naris (Panchen 1967) to support the posterior wall of the tubular vestibulum, the first of three major subdivisions of the tetrapod nasal cavity (Parsons 1967). Prominent septomaxillae are present in *Acheloma* (Text-fig. 1A; Dilkes and Reisz, 1987) and *Phonerpeton* (Text-fig. 1B; Dilkes 1990) at the junction between the anterior and posterior portions of the external naris. Hence, the anterior division of the trematopid external naris was the functional narial opening.

The term antorbital vacuity was finally abandoned by Romer (1947) who referred to the entire opening as a posteriorly elongated external naris. All subsequent authors have followed Romer's terminology.

In the most recent consideration of the trematopid nasal chamber and the elongated external naris, Bolt (1974a) thought it unlikely that the narial flange subdivided the nasal capsule to either increase epithelium or separate functionally different chambers because among living amphibians most flanges that protrude into the nasal sac are derived from the cartilaginous nasal capsule and not the surrounding dermal bones. Instead, he proposed that the nasal capsule was situated lateral to the narial flange. Placement of the nasal capsule lateral to the flange required a reinterpretation of a raised ridge on the dorsal surface of the palatine that Bolt observed in the rostrum of a small trematopid skull. This palatine ridge (Text-figs 3–5) has been reported in other temnospondyls (e.g. *Eryops*: Swain 1941; *Parotosuchus*: Warren 1980, fig. 3A) and is generally thought to brace the posterior wall of the nasal capsule. Bolt argued that the palatine ridge was not a necessary indicator of the shape of the capsule and perhaps marked the presence of some other cartilaginous structure.

Bolt (1974a) also examined the possible existence of a specialized narial gland in trematopids and

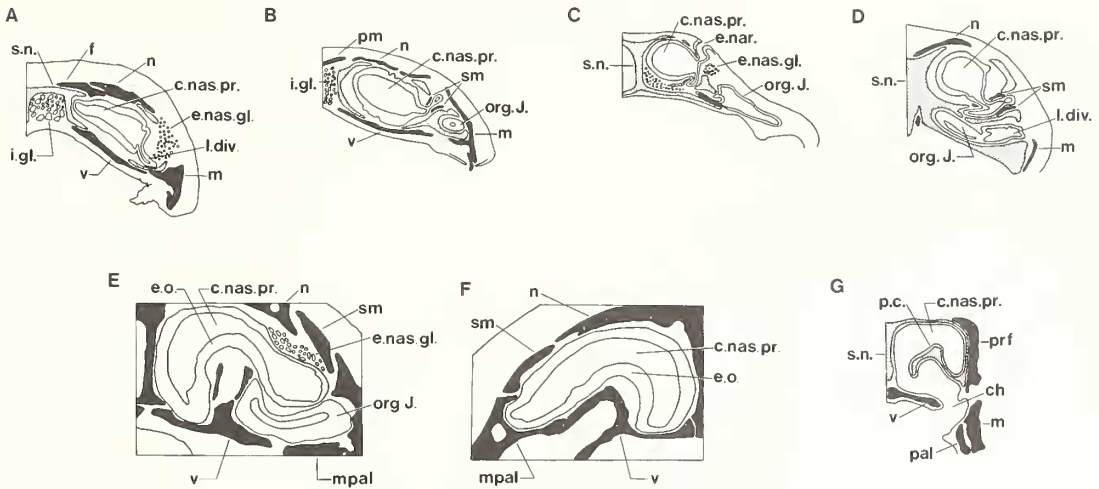
argued that a salt gland, possibly one that was homologous to the external nasal gland of reptiles, was the most probable candidate for these terrestrial amphibians. He proposed that this salt gland expanded laterally, presumably to enhance its efficiency as a salt-excreting organ. Expansion was restricted to a lateral direction because medial expansion would force the nasal capsule against the narial flange. As the salt gland expanded laterally, the external naris elongated posteriorly to accommodate the larger gland. This narial elongation had profound consequences for the mechanical bracing of the antorbital region. According to Bolt, forces generated during feeding would be concentrated in the antorbital region and the reduction of this region to a bar by the expansion of the external naris would weaken the skull. The narial flange was recruited to act as a strut to brace the weakened antorbital region. Bolt pointed out that the dissorophid narial flange probably also had a mechanical role in bracing sutural contacts between rostral bones and that his hypothesis for the trematopid narial flange was based upon a change in the pattern of cranial stresses.

There are several difficulties with the above scenario. Only meagre osseous evidence in the form of impressions exists on the inner surfaces of dermal bones for a reconstruction of the cartilaginous nasal capsule in trematopids. No details, such as size, shape, or even existence of possible fenestrae can be determined. Thus, there is no *a priori* reason to assume that constraints on medial expansion of an external nasal gland left lateral expansion as the sole option. Presumably, since the choana occupies the entire space between the septomaxilla anteriorly and the contact of the narial flange with the antorbital bar posteriorly, a lateral salt gland would have been above the choana. Any expansion of this gland could occur in a number of different directions, including (but not exclusively) laterally. To argue for a restriction of expansion to one specific direction would require detailed knowledge of the soft anatomy of the nasal region that is not available.

Even if the existence of a laterally expanded external nasal gland is accepted, no clear causal connection between its expansion and the elongation of the external naris can be demonstrated. All reptilian salt glands share a common histology and embryology despite the independent origins of these glands among different groups of reptiles (Parsons 1970; Dunson 1976). Reptilian salt glands are branched or compound tubular glands and grow by repeated branching to reach their adult shape late in embryology. All subsequent growth of the gland keeps pace with that of the skull. The naso-labial gland of plethodontid salamanders is also a branched tubular gland that grows by occupying any available cavity or foramen without affecting cartilaginous or osseous structures (Whipple 1906). If the hypothesized salt gland of trematopids was also a tubular gland, then it presumably grew in a fashion similar to the reptilian salt gland and the plethodontid naso-labial gland. It is, therefore, unnecessary to hypothesize loss of bone as a consequence of salt gland expansion. Nor is there strong evidence for a positive correlation between the presence of an enlarged external nasal gland and an elongated external naris in an extant tetrapod. For example, dermal bones around the external naris of *Varanus* are reduced so that the opening is greatly enlarged and the nasal capsule is visible (Bellairs 1949). Skin and connective tissue cover the exposed portion of the nasal capsule. The external nasal gland of *Varanus* is not enlarged and is located within the conchal space behind the external naris.

Terrestriality and nasal anatomy

In a comparative study of the amphibian nasal region, Jurgens (1971) concluded that, contrary to previous assertions (e.g. Jarvik 1942), there are numerous similarities between the nasal capsules of the three recognized living orders. Jurgens identified several intermediate stages in some anurans and urodeles which he believed demonstrated an especially close phylogenetic link between these groups. Differences between representatives of each group could be explained by the formation and elaboration of accessory nasal sacs. The degree of elaboration of accessory nasal sacs was correlated positively with increased terrestriality, and Jurgens hypothesized that the adoption of a terrestrial lifestyle was the selective agent responsible for the evolution of accessory nasal sacs. The simplest accessory nasal sac of amphibians is the lateral diverticulum (lateral nasal sinus) of primitive (aquatic) urodeles which forms a simple ventrolateral extension of the cavum nasi proprium and



TEXT-FIG. 7. Transverse sections of nasal chambers in representative extant ectothermic vertebrates. A, urodele *Salamandra maculata* (redrawn from Seydel 1895). B, urodele *Ambystoma maculatum* (redrawn from Jurgens 1971). C, anuran *Rana esculenta* (redrawn from Seydel 1895). D, anuran *Alytes obstetricans* (redrawn from Jurgens 1971). E–F, gymnophionan *Ichthyophis glutinosus* (drawn from photographs in Badenhorst 1978). G, sphenodontid *Sphenodon punctata* (redrawn from Hoppe 1934). Black areas are bone and stippled areas are cartilage. Not drawn to scale.

remains entirely continuous with the cavum (Text-fig. 7A). In contrast, the lateral diverticulum and organ of Jacobson of terrestrial salamanders is subdivided from the cavum to varying degrees by vertical or inclined cartilages (Text-fig. 7B). Separation of the lateral diverticulum from the cavum and the isolation of the organ of Jacobson in a subchamber of the lateral diverticulum is developed further in terrestrial anurans (Text-fig. 7C–D).

Trematopid amphibians are generally considered to be terrestrial carnivores (Olson 1970; Bolt 1974a; Dilkes 1990) largely on the basis of the presence of caniniform teeth, extensive cranial and postcranial ossification, slender and relatively long limb elements, large otic notches, and the absence of lateral line grooves or pits. Dissorophids share many of these general adaptations and they form the other major group of terrestrial temnospondyls. If it is assumed that terrestriality was an important selective agent in the evolution of dissorophids and trematopids and if one also accepts the hypothesis of Jurgens (1971) that terrestriality among lissamphibians was the key selective agent responsible for the evolution of accessory nasal sacs, then one may speculate that dissorophids and trematopids had accessory nasal sacs. As the lateral diverticulum is the one accessory nasal sac from which the others have apparently evolved, the search may be limited to finding evidence for this nasal sac.

The narial flange would appear to be the only evidence for the presence of a lateral diverticulum in Palaeozoic dissorophoids since it is the only ossified structure that projects into the nasal chamber. However, the arguments by Bolt (1974a) on the relative contributions of dermal bone and cartilage to internal nasal projections would seem to suggest otherwise. To determine whether or not the dissorophoid narial flange does constitute evidence for a partly isolated lateral diverticulum, two issues must first be addressed. These issues are: (1) the likelihood of an ossified as opposed to cartilaginous internal nasal projection in temnospondyls; and (2) whether or not the dissorophoid narial flange was actually inside the nasal capsule.

First, it is true that the cartilaginous chondrocranium of anurans and urodeles is more extensive than the surrounding dermal bones and provides the principal support for the olfactory organ (Text-fig. 7A–D). The chondrocranium in these amphibians would then be expected to produce any

internal projections, and, as observed by Jurgens (1971), cartilage is indeed the source for the varied internal nasal flanges that appear in terrestrial amphibians. However, any assumption that extinct terrestrial temnospondyls would necessarily follow the same pattern is questionable. Paedomorphosis was probably an important factor in the phylogeny of extant amphibians (Bolt 1977a, 1979; Milner 1988), so the rarity of dermal flanges in the nasal chamber of anurans and urodeles may be a consequence of their inheritance of a larval level of ossification. Adult non-lissamphibian dissorophoids with their highly ossified skulls may have had a different relationship between the dermal skull and chondrocranium since they would represent a line of development divergent from the one taken by extant amphibians. Support for this hypothesis is provided by the extant limbless, burrowing amphibians known as caecilians. The extent of dermal cranial ossification is enhanced secondarily relative to anurans and urodeles to produce the characteristic solidly ossified skull roof (Wake and Hanken 1982). Consequently, the chondrocranium is largely resorbed during development, and the olfactory organ is supported primarily by dermal bones of the roof and palate (Text-fig 7E–F), in particular the maxillopalatine, septomaxilla, and vomer (Duellman and Trueb 1986). The prominent eminentia olfactoria on the floor of the olfactory sac is supported in anurans and urodeles primarily by the floor of the nasal capsule (solum nasi) with a small contribution from the vomer (Jurgens 1971). In caecilians, on the other hand, primary support for the eminentia olfactoria is the vomer (Text-fig. 7E) with a lateral contribution from the maxillopalatine (Text-fig. 7F). Caution is advised though when applying these observations to temnospondyls because internal impressions on the fossilized bone suggest a uniformly broad and plate-like ethmoid in addition to the robustly ossified skull (Roček 1990). Nonetheless, the projection of a dermal flange into the nasal capsule of dissorophoids is consistent with the pattern of cranial development in extant amphibians.

Second, contrary to the suggestion of Bolt (1974a) the dorsal ridge on the palatine does represent the approximate position of the posterior wall of the nasal capsule. The hind wall of anuran and urodelan nasal capsules is termed the postnasal wall and is connected to the palatoquadrate laterally by the processus maxillaris posterior and medially by the commissura quadrato-cranialis anterior (Jurgens 1971). In temnospondyls, the postnasal wall was separated from the palatoquadrate by the palatine ridge (Roček 1990). A postchoanal depression immediately anterior to this palatine ridge in species of *Branchiosaurus* held the lateral portion of the postnasal wall (Watson 1940; Boy 1978; Roček 1990). The course of the palatoquadrate in branchiosaurids can be traced along a distinct groove on the dorsal surface of the pterygoid to a groove on the palatine along the posterior side of the palatine ridge. This groove on the palatine probably accommodated the processus maxillaris posterior and the commissura quadrato-cranialis anterior. A similar pair of grooves on the pterygoid and palatine of trematopids probably carried the same cartilaginous structures. Trematopids lack a postchoanal depression on the palatine, but the anterior side of the palatine ridge is concave and, as in branchiosaurids, probably held the postnasal wall. Since trematopids and dissorophoids have prominent palatine ridges and the narial flange of each family is located entirely anterior to this ridge, the dissorophoid narial flange was clearly within the confines of the nasal capsule. Thus, the narial flange subdivides partly the nasal chamber, and the slightly smaller region above the choana was probably a lateral diverticulum.

Although the presence of a narial flange may be linked to terrestriality, differences in the shapes of the trematopid and dissorophid flanges suggest that some additional agent, perhaps dietary, directed the details of their construction. Bolt (1974c) argued that the magnitude of the stresses imposed upon the skull of an early tetrapod during feeding are proportional to the size and position of the palatal tusks and marginal teeth that engage the prey. According to Bolt, the orbits would concentrate stresses within the antorbital and postorbital regions. Thus, the marked contrast in dental morphology between trematopids and dissorophids may have been an important factor in the evolution of the distinctive trematopid narial flange. Teeth of small dissorophids tend to be small, uniform in size, and peg-like with the crowns varying from monocuspid to bicuspid (Bolt 1977a). Larger dissorophids have large, monocuspid teeth that remain relatively uniform in length. Trematopids, however, are characterized by their caniniform teeth on the premaxillae and maxillae

(Dilkes 1990). Maxillary caniniform teeth are located anterior to the orbits, just in front of the palatine tusks. As the caniniform teeth and palatal tusks would first contact the food item, they would concentrate cranial stresses in the antorbital region. If the above assumption of a correlation between stress concentration and the size and location of the teeth involved in prey capture is valid, then the stresses imposed on the antorbital region may have been far greater in trematopids than dissorophids. The establishment of a contact between the narial flange and narrow antorbital bar would perhaps transfer these stresses away from the bar, as suggested by Bolt (1974a). The functional replacement of that portion of the antorbital region behind the external naris by the narial flange possibly led to the subsequent loss of this region by the gradual posterior expansion of the narial opening.

Support for the phylogenetic origin of the trematopid narial flange and elongated external naris by development of caniniform teeth can be found in the ontogenetic sequence for the rostrum outlined in this paper. It is assumed that the phylogenetic and ontogenetic stages would be comparable because in each instance there is a shift in habitat preference from aquatic to terrestrial. Both the early ontogenetic appearance of a narial flange prior to elongation of the external naris and the coincident development of caniniform teeth and the elongation of the external naris fit major stages in the proposed scheme of trematopid phylogeny, but not the hypothesis of Bolt (1974a) in which elongation of the external naris and development of the trematopid narial flange are concurrent. Not all stages are, however, recapitulated. For example, the hypothesized differentiation of a dissorophid-like narial flange to a trematopid narial flange does not occur during the observed stages of ontogeny even though the proposed causal agent of caniniform teeth exhibits a clear progressive development. However, it is possible that the relative ontogenetic timing of the narial flange might have been modified in dissorophoid phylogeny. Presence of a narial flange in a presumably aquatic larval dissorophoid (Dilkes 1991) is perplexing if a narial flange is an adaptation for terrestriality. One possible explanation is a heterochronic (peramorphic) shift in the formation of the narial flange to an earlier point in ontogeny. A peramorphic change could be achieved either by a later termination or earlier beginning of growth or an acceleration of growth (McKinney *et al.* 1990).

POSSIBLE PHYSIOLOGY OF THE TREMATOPID NARIS

Nasal systems of terrestrial vertebrates, in addition to their role of nasopharyngeal breathing, must also detect often low concentrations of air-borne molecules that diffuse rapidly, and act as a site for the conditioning of inspired air through filtering, warming, and humidification (Romer and Parsons 1986). Exchange of heat and water between inhaled and exhaled air and the nasal walls is found in all terrestrial vertebrates (Schmidt-Nelson 1983). Significant quantities of heat and water that would otherwise be lost to the environment through exhaled air can be recovered in the nasal sacs of endotherms (Schmidt-Nelson *et al.* 1970) and ectotherms (Murrish and Schmidt-Nelson 1970).

The efficiency of the counter-current exchange mechanism in the nasal chamber of terrestrial vertebrates is enhanced if the surface area for exchange is increased, the distance from the centre of the air flow to the nasal wall is decreased, and the velocity of the passage of air is diminished. Conchae, defined as any curved projection of the lateral wall of the nasal chamber (Romer and Parsons 1986; Test-fig. 7E), are responsible for the facilitation of heat and water conservation in the nasal chamber. All amniotes, with the exception of turtles, possess conchae in their nasal chambers (Parsons 1967). Amphibians lack conchae (Jurgens 1971). Experimental data show that the efficiency of the reclamation of heat and water is correlated with the sophistication of the conchae (Murrish and Schmidt-Nielsen 1970; Schmidt-Nielsen *et al.* 1970).

Removal of heat from exhaled air results in important metabolic savings for endotherms (Schmidt-Nielsen *et al.* 1970); however, since ectotherms rely upon external heat sources any savings in their energy budget by this mechanism would probably be secondary to water conservation (Murrish and Schmidt-Nielsen 1970). It is assumed that early tetrapods were ectothermic, as the presence of growth rings in their bone would suggest (Enlow and Brown 1956).

Therefore, water rather than heat conservation could have been an important selective agent in the evolution of the nasal region in Palaeozoic amphibians and reptiles.

Little detailed information can be gained directly from fossils on the complexity of a cartilaginous nasal capsule, though in the case of temnospondyls it is possible to reconstruct the general aspects of their ethmoidal cartilages (Roček 1990). Despite these inherent difficulties, it is clear that the presence of a bony flange which projected into the nasal capsule of dissorophoids would have increased the surface area of the nasal epithelium and decreased the speed of air flow through the nasal sac and, thus, aided the recovery of water. The rate of air flow is also an important variable in determining the level of olfactory responses (Mozell *et al.* 1984). With the exception of mammals, most of the air that passes through the nasal sac of amniotes and anamniotes crosses the olfactory epithelium. An increase in the rate of air flow has a negative effect upon olfactory response because the probability of an odorant molecule being absorbed by the mucus layer is decreased as the velocity at which the molecules strike the mucus is increased. Thus, any obstructions to the air flow, such as a narial flange, would enhance olfactory responses by increasing the proportion of odorant molecules that penetrate the mucus and are detected by the receptor cells. Conservation of water and the enhancement of olfaction may have been complementary factors in the evolution of the dissorophoid narial flange which would then have fulfilled an analogous role to the concha of reptiles.

No reference to a specific environment is implied in this hypothesis of physiological analogy between reptilian conchae and the dissorophoid narial flange. Dissorophoids are a common component of sites in the southwest of the United States that are interpreted as mixed load river systems (Berman *et al.* 1987) and ponds (Sander 1989) whereas more northerly sites in North America have yielded only a few dissorophoids from settings such as infilled abandoned river channels (Hook and Ferm 1988) and deltas (Baird *et al.* 1985). The presence of a narial flange within the nasal chamber of dissorophoids is interpreted as evidence for a more terrestrial lifestyle although they apparently remained associated with water, in particular rivers and ponds.

None of the above arguments discounts the proposal by Bolt (1974a) of a salt gland in trematopids derived from an external nasal gland. Amphibians and reptiles have homologous external nasal glands (Parsons 1959), and the common presence of this gland in extant tetrapods suggests that it is probably plesiomorphic for the group. Salt glands are an important extrarenal route for the elimination of excess ions, especially potassium, taken in through the diet or accumulated as a result of desiccation (Templeton 1964; Dunson 1976; Minnich 1982). However, salt glands are absent or greatly reduced in size in some terrestrial reptiles that accumulate large quantities of ions through their diet. Furthermore, terrestrial reptiles typically excrete nitrogenous wastes in the form of urate which has the advantages of binding large quantities of the same ions removed by salt glands and allowing significant amounts of water to be resorbed through the walls of the bladder and cloaca (Minnich 1982). Clearly, there is no evidence in the fossils to suggest that dissorophoids or any other extinct terrestrial vertebrate used urate excretion. Nonetheless, given the reliance of any physiological hypothesis for an extinct vertebrate upon extant representatives, the importance of urate excretion in terrestrial reptiles and at least two genera of arboreal anurans (Shoemaker 1988) and reduction or absence of salt glands in some desert-dwelling lizards weakens arguments for a strong positive correlation between terrestriality and the presence of a salt gland.

CONCLUSIONS

Development of the distinctive narial flange of trematopid amphibians occurred early in postmetamorphic ontogeny. Posterior elongation of the external naris and the differentiation of caniniform teeth on the premaxillae and maxillae are subsequent growth stages that reach their fullest expression only in adults. Hence, at present, only the shape of the narial flange is a reliable character for the identification of juvenile postmetamorphic trematopids. The narial flanges of trematopids and dissorophoids are reinterpreted as projections into the nasal sac that enhanced water conservation and olfactory sensitivity in a manner analogous to the conchae of amniotes. Although

amphibians lack conchae, they show evidence of a positive correlation between terrestriality and the presence of cartilaginous projections into the nasal sac. As the moist skin of extant amphibians is the primary site for the loss and resorption of water (Duellman and Trueb 1986), the cartilaginous projections probably improve only olfaction. Conchae, narial flanges, and cartilaginous projections are independent evolutionary attempts to improve olfaction and, in the case of the first pair of structures, conserve water among terrestrial tetrapods.

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